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ART. VIII.-Oscillatory Adjustments in the Animal Body.

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Ostwald has pointed out that if any system be self-adjusting the equilibrium attained must necessarily be oscillatory. As an illustration of this, he cites the thermostat, where the regulator shuts off the heat supply when a certain standard temperature has been exceeded. The result of this withdrawal is a fall of temperature below the desired level; to be succeeded by a rise and so forth. The better the regulating mechanism the smaller are the oscillations, and the best device is that in which the amplitude of the variation is reduced to a negligible quantity. As Ostwald points out, this principle can be extended to human affairs; in politics, for instance, there is always the tendency for opinion to oscillate between radical and conservative positions; in the realm of the aesthetic standards of taste move to and fro between the florid and the austere. I purpose to apply this principle to some aspects of animal physiology, for in the animal body we find numerous adjustments which are relatively constant, and which maintain constancy by self-regulating mechanisms. Amongst the many physiological landmarks in evolution the transformation of a variable into an invariable (temperature, osmotic pressure, etc.) has been conspicuous, but we are compelled to assume that, however close to a fixed standard the adjustment is made, if a self-regulating mechanism is at work a state of oscillatory equilibrium has been established. A number of instances may now be discussed.

I. Respiration.—We owe to Haldane¹ and his school the discovery of the chemical regulation of pulmonary ventilation. If metabolism is not too active as it is in violent exercise there is a remarkable constancy shown in the CO_2 tension of the alveolar air. This means a similar constancy in the tension of CO_2 in the arterial blood, and the standard attained is just that which is adequate to excite the respiratory centre in the medulla oblongata. It does not affect the argument if we hold that CO_2 is the specific excitant, or whether it is the hydrogen ion which is causative. Now, in health, the oscillations above and below the mean of quiet respiration are so damped that they escape recognition (though it is just possible that

¹ The Regulation of the Lung Ventilation. J. Physiol., vol. 32, p. 225, 1904.

yawning may find a partial explanation here), but in disease, as Haldane pointed out later, the oscillations may become large and obvious, producing the Cheyne-Stokes breathing, which is so striking a clinical sign. Here we find conformity to the rule that an inadequate or deranged regulator will be made manifest by an increase in the amplitude of the oscillation.

II. Body Temperature .-- A great advance in evolution was the rise of the homoiothermal bird and mammal. In poikilothermal creatures metabolism is a function of the air temperature, and comes almost to a standstill in the winter of certain climates. A poikilothermal man could not make definite plans or enter into definite contracts for the performance of work except in the tropics as the ability to labour would rise and fall as the air was warm or cold. Now the temperature of a bird or mammal is not absolutely constant. Vigorous muscular movement, as is well known, may, even in an English winter, drive the temperature up to fever pitch; normality is resumed quickly if the air is cold, slowly if the air is hot and humid. The temperature chart of a healthy human being is by no means a straight line. Even when metabolism is kept fairly constant, as when the subject of the experiment remains fasting in bed, a marked diurnal oscillation is apparent, which may have an amplitude of as much as 0.8°C.¹ Whether this oscillation is that due to self-regulation or is more properly a periodicity effect, is, however, not very clear. Much more likely to be the oscillations in question are those small irregular waves displayed when thermoelectric records are graphically taken. Again, we find that a deranged mechanism will produce an exaggerated amplitude of rhythm. In convalescence from an illness, particularly an illness accompanied by fever, exertion that would not in health affect the adjustment, is sufficient to provoke a decided elevation of temperature, and lead to copious sweating, which, in its turn, can very easily produce subnormality when the exercise ceases.

III. The Muscular System.—It will be evident that if the position assumed by a limb is one extreme of movement, if, for instance, extension be carried as far as the ligaments on the flexor side will allow, the fixation here is mechanical, and no oscillation need be expected. In reflex postural contraction it is also probable that an arhythmical fixation is present for the tension may here be purely elastic, the contractile substance being fixed by a hook mechanism (Grützner)², or through gel formation (Sherrington)³.

2 See Bayliss, Principles of General Physiology, 1915, p. 534.

¹ See article Die Wärmeökonomie des Körpers, by R. Tigerstedt in Nagel's Handbuch,

³ Postural Activity of Muscle and Nerve. Brain, 1915, vol. 37, p. 191.

But when a limb assumes a special directive position through voluntary muscular action there is no rigid attachment, and the constancy of the direction must of necessity be adjusted by the proprioceptive system reinforced by vision or touch, or occasionally by the proprioceptive system alone. Here it is impossible that oscillation could be avoided, and oscillation is assuredly found. Moreover the better the mechanisms involved-the steadier the nerves in popular parlance-the smaller and more uniform are the oscillations. This is well displayed in rifle shooting, particularly when the barrel is unsupported. A good shot is aware of the tremor but he is able to keep it regular and of small dimensions. Similarly in all skilled actions, and skill will always mean precision of spatial and temporal relations, a high degree of efficiency is only possible if the oscillations arising from the adjusting mechanism remain small. Equilibrists and wire-walkers are definitely aware of the oscillatory effect, and consciously resort to fine rhythmic movement to keep the centre of gravity not statically above the small base of support but moving to and fro on either side. Excitement, selfconsciousness, lack of experience, strain, fatigue, etc., may in the healthy body produce an extensive increase in the range of oscillation, whilst that exaggeration due to alcoholism, cerebellar disease, senility, neurasthenia, etc., is well known. A small amount of swaving of the upright body when the eyes are shut has often been observed in health, but a marked oscillatory movement has a high diagnostic value. The position of the eyeball is maintained by muscular contraction, guided by macular vision and the proprioceptive information sent up from the eves muscles. But when a static object is regarded steadily the visual axis is not immobile: there is a slight range of tremor. That this delicate oscillation plays some part in art, especially pointilistic art, has been suggested by H. G. Keller and J. J. R. Macleod¹. Again, it is possible that in nystagmus we may find the pathological amplification of a normal rhythm2. That a voluntary fixation of a limb (using the term limb in its widest sense) must of necessity be oscillatory is not usually assumed in physiological literature, yet a little consideration will show that this must exist. In dealing, therefore, with the rhythm of neural discharge from the central nervous system to the muscles, two possible causes must be borne in mind. There may be an intrinsic periodicity in the nerve cell or nerve cell complex-i.e., rhythmic discharge of each nerve cell or rhythm due to sequence of

¹ Popular Science Monthly. November, 1913.

² This has been stated precisely by Coppez. Archives d'Ophthalmologie, vol. 33, p. 545.

one nerve cell discharging after the other. This is the causative factor usually assumed. But the rhythm due to absence of mechanical fixation and absolutely necessitated by the adjustments based on sensory impressions is left out of count.

IV. The Blood Constants .- The blood of the higher animals displays remarkable constancy in a number of its characters. Determinations of hydrogen ion concentration have shown that the range of reaction, despite almost gross variations in the reaction of food and of metabolites, is exceedingly small. Here the kidney and lungs are the organs entrusted with the standardisation, or, at least, with the fine adjustment of the standardisation. There is similarly a constancy with respect to osmotic pressure, metallic balance and water content, and again the kidney is the regulating organ. If an oscillation in any of these properties were sought for it would be in the blood from the renal vein, but one might well expect the oscillations to be so small and so damped that they would escape detection. Yet it is surely possible that pathological conditions might exist which would magnify such oscillations and make them detectable and of import to the functioning of the tissues of the body generally.

Arteriolar vaso-constriction is a local variable adjusted to the varying action of gravity on each part of the body and to the varying call for blood from the organs as they are severally excited. Yet there is a mean blood pressure and self-regulating devices, such as the depressor nerve or the direct action of high pressure on the medulla, have been proved to exist. Though once more the oscillations produced may be too small and too damped to be made manifest, it is again possible to assume that they may be greatly exaggerated in pathological states.

What determines the total quantity of blood in the body, the concentration of plasma proteins, and the number of formed elements, physiology as yet has not determined, but if self-regulating mechanisms are at work, the same argument applies.

The above are a few only of the self-adjusting processes in the body. There are many others not touched upon. One has only to think of the reflex excitation of the lachrymal gland, which is so finely adjusted that both dryness and excessive moisture of the cornea are avoided, of the secretion of mucous surfaces, of the growth of the skin *pari-passu* with frictional loss and such like, to realise that self-adjustment is the rule and not the exception. And in all self-adjusting systems, we may venture to state, rhythm, if not apparent, is latent, and can be brought into prominence by pathological changes.